Foraging Patterns of *Cyphoma gibbosum* on Octocorals: the Roles of Host Choice and Feeding Preference

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Abstract. The distributions of small, relatively slow moving grazers are often portrayed as expressions of feeding preference. However, more careful analysis of such distribution patterns in concert with measurements of feeding suggests that the distribution patterns of the gorgonian-eating snail *Cyphoma gibbosum* may not reflect the influence of feeding preference alone. *C. gibbosum* is common at many sites in the San Blas Islands, Panama, occurring at densities ranging from 2–30 snails/100 m². The movements and feeding of 244 labelled snails were followed at three sites in the San Blas during the summers of 1984–1986. Relative to gorgonian colony abundance *C. gibbosum* were preferentially found on colonies of *Pseudopterogorgia* spp., *Pseudoplexaura* spp., and *Plexaura homomalla*. Snails exhibited the same preferences in their movements between colonies, and often remained longer on those same gorgonian species.

The prolonged occupancy on colonies of some species was the dominant factor controlling the amount of tissue consumed from any one species. Thus preferences for different host gorgonians also established total feeding. Preferences loosely correlated with the organic content of the different gorgonian species (% ash-free dry weight), but do not explain the observed preference for *P. homomalla* colonies. Host preferences were not reflected in feeding rates. Feeding rates on *Pseudopterogorgia* colonies were lower than on other frequently occupied species. The weak correspondence between feeding rates and occupancy preferences suggests that factors in addition to feeding such as social interactions and predator avoidance may play an important role in establishing host preferences.

Introduction

Grazers play an important role in controlling the abundance of a wide variety of marine benthic algae and invertebrates (Ogden *et al.*, 1973; Sammarco *et al.*, 1974; Glynn, 1976; Lubchenco, 1978; Hay, 1981; Lubchenco and Gaines, 1981; Lewis, 1986), and thus the preferences of grazers can have important effects on benthic community structure. Recent analyses of prey preferences of marine grazers have emphasized the importance of prey quality, particularly the presence of secondary compounds, in establishing grazer preference (Gerhart, 1984; Steinberg, 1985; Targett *et al.*, 1986, Hay *et al.*, 1987). However, prey choice in many species may not be a simple feeding choice (Hay *et al.*, 1987). In many communities the grazers are small sedentary species that spend prolonged periods of time on single prey individuals. These grazers' prey may serve many functions, and preferential use of some prey species may reflect selective pressures quite different from considerations of feeding alone. It may be more accurate to describe the prey of these species as hosts, and a fundamental question that must be asked in these cases is whether observed host preferences can be adequately described in terms of feeding alone. In this paper we address this question by examining the foraging behavior of the ovulid gastropod *Cyphoma gibbosum* on Caribbean gorgonians.

Since the distribution of *C. gibbosum* on gorgonians is also the distribution of *C. gibbosum* at its feeding sites, *C. gibbosum* distributions have been approached as for-

aging problems (Birkeland and Gregory, 1975; Harvell and Suchanek, 1987). If considered solely in the context of grazing, gorgonian choice by *C. gibbosum* is analogous to models of which patch a forager should choose and how long it should remain in it (Pyke *et al.*, 1977; Krebs, 1978; Pyke, 1984). However, the patches that *C. gibbosum* uses, *i.e.*, gorgonians, serve as sites for protection, mating, and egg deposition as well as food sources. These behaviors may have a large effect on *C. gibbosum* foraging behavior.

The amount of feeding that occurs on a given gorgonian species is controlled by several potentially independent behaviors: host selection, residence time on the host, and grazing rate. If feeding is the primary factor influencing foraging, then the same gorgonian species would be favored regardless of which behavior is observed. However, movement patterns and the amount of time spent on a colony may also reflect preferences for functions such as mating and egg laying. Therefore, different species could be identified as preferred "prey" depending on which behavior was examined. The extent to which the three different components of foraging identify similar preferences may indicate whether the preferences are best described as preferences for different prey species or simply as host preferences. In characterizing the foraging patterns of *C. gibbosum*, we partition the feeding process into its component behaviors and ask whether species preferences exist and whether they should be termed feeding preferences.

Previous work

A number of researchers have described the activities of *C. gibbosum* (Kinzie, 1970, 1974; Birkeland and Gregory, 1975; Hazlett and Bach, 1982; Harvell and Suchanek, 1987). Although these studies have uniformly verified the specialization of *C. gibbosum* on gorgonians, the differences among reported species preferences are striking. Kinzie (1970) considered *C. gibbosum* to be the principal grazer of gorgonians at Discovery Bay, Jamaica, where for instance, he observed a large *C. gibbosum* aggregation denuding several gorgonian colonies. Kinzie (1970, 1974) did not observe preferences in either the distribution of snails or paired choice experiments.

Birkeland and Gregory (1975) observed the movement and feeding habits of marked *C. gibbosum* during three weeks of intensive study using the Tektite habitat at Lameshur Bay, St. Johns, U. S. Virgin Islands. They report that *C. gibbosum* were found preferentially on *Gorgonia* spp. and *Eunicea succinea,* and that in experiments *C. gibbosum* regularly chose *Gorgonia* spp. over other species. They also found that feeding rates varied with prey species. Feeding rates were greatest among snails on *Gorgonia* spp., but feeding rates were among the lowest on the second most commonly occupied species, *E. succinea.* Harvell and Suchanek (1976) followed marked individuals over a two week period at Salt River Canyon, St. Croix, U. S. Virgin Islands. They found no significant selectivity in the movements of *C. gibbosum,* but they found that snails remained significantly longer on the "*Plexaura* group" (*P. flexuosa, P. homomalla,* and *Pseudoplexaura crucis*) than on *Eunicea* and *Muricea* spp. There were no significant differences in the length of feeding scars generated by snails, but there were significant differences in the depth of scars on different species.

In addition to variation in observed preferences Birkeland and Gregory (1975) and Harvell and Suchanek (1976) report patterns of snail distribution and movement which do not always correlate with observed grazing. This variation underscores the need for longer term multi-site observations which carefully partition the different components of the feeding process.

Materials and Methods

The study was conducted in the San Blas Islands, Panama, at the facilities of the Smithsonian Tropical Research Institute. Observations of *C. gibbosum* feeding were made at three small patch reefs located within several kilometers of San Blas Point. A detailed map of the area is contained in Robertson (1987). The first reef, Macaroon (Porvenir-26 in Robertson, 1987), is located south of a channel through the barrier reef. The reef is 3–4 m deep and is an elliptical hardground approximately 50 m by 30 m which rises 1–2 meters above the surrounding *Thalassia* bed. The reef fauna is dominated by large colonies of the gorgonians *Pseudoplexaura porosa* and *Plexaura flexuosa* and scattered heads of the scleractinians *Diploria strigosa, Siderastrea siderea,* and *Agaricia agaricites.* Gorgonians are the most conspicuous members of the benthos at Macaroon. The area chosen for study was located in the southwest quadrant of the reef.

The second reef, Korbiski (Korbiski-1, SE in Robertson, 1987), is a large reef and reef-flat complex approximately 500 m long and up to 250 m wide. Most of the area is a sand and *Thalassia* reef-flat. The edge of the flat is marked by a narrow band of heavy coral cover (*Agaricia* spp., *Millepora* spp., *Porites furcata, Siderastrea siderea, Diploria* spp.), which grades into a slope with scattered head corals (*Montastrea annularis, Montastrea cavernosa, Diploria strigosa, Colpophyllia natans*). Gorgonians are common on the slope where they are associated with head corals, and at the top of the slope where dense aggregations are found on consolidated coral rubble. The study site was located in an area of mixed hardground and sand 1.0–2.5 m in depth at the northeast tip

of the reef. The gorgonian fauna at the site was dominated by *Plexaura* A (see Lasker, 1984, for description of this uncertain species), *Pseudoplexaura porosa, Plexaura homomalla,* and *Plexaura flexuosa.*

The third reef, Pinnacles (Pico Feo-14 in Robertson, 1987), is an area of mixed sand and hardground substrate with scattered clumps of hard coral (*Montastrea annularis, Colpophyllia natans, Porites* spp., *Agaricia* spp.). These clumps, or pinnacles, of coral rise from a depth of 10 m to within 0.5 m of the surface. The gorgonians *Pseudoplexaura porosa, Eunicea* spp. and *Plexaura homomalla* are common on the hard substrate created by the scleractinians. The site chosen for the study was a gently sloping area of sand and coral substrate at 5–7 m depth.

Censuses of *C. gibbosum* were conducted within a single arbitrarily selected 100 m² area at each site. The areas were marked and a grid laid at 2 m intervals. All gorgonian colonies within the 10×10 m areas were identified to genus and/or species and their heights measured. Colonies which were visited by *Cyphoma* during the study were tagged and their location mapped. Detailed monitoring at the sites was conducted during 1984 (June 8–August 8), 1985 (April 6–June 26), and 1986 (June 7–July 19). During 1984 and 1985 all the sites were searched for *Cyphoma* at approximately three-day intervals. Censuses were conducted weekly during 1986. Newly discovered individuals were removed from the gorgonian colony; the shell scored with a triangular file (after Harvell and Suchanek, 1987); and the snail immediately placed back on the gorgonian. Using a system of markings which ran either perpendicular or parallel to the snail's anterior-posterior axis it was possible to code each shell with a unique mark. At Macaroon, for instance, 61 different individuals were so coded in 1985. The markings were permanent and one individual at Macaroon was observed in each of the three years of observations. The shells of small *Cyphoma* (<1 cm in length) were too thin to score. These individuals were identified on the basis of their size and location. No more than two snails were followed in this manner at any one site.

The distribution patterns of *C. gibbosum* on gorgonians at the different sites were analyzed in a variety of ways. First, the data were analyzed for preference based on the number of times snails were observed on the different species. We call these data occupancy. Second, preferences in choosing colonies were determined by only considering observations in which a snail changed colonies. We call these data movements. Finally the length of each visit to a colony was determined. We call this residence time.

Preferences in occupancy and movements were analyzed with respect to gorgonian abundances using G-tests

(Sokal and Rohlf, 1969). In presenting our results we use the ratio of observed to expected occurrences as an index of preference. The observed:expected ratio suffers from a number of shortcomings (Chesson, 1978). However, we use it here because our test statistic G is in large part derived from observed:expected ratios. Indices such as Ivlev's *e* (Ivlev, 1961) use Chi-square statistics, which cannot be partitioned accurately into different factors (Sokal and Rohlf, 1969).

Distributions of *C. gibbosum* on gorgonian colonies were compared to species abundances (Fig. 1). Ideally gorgonian abundance should be measured in a manner that mirrors the snails' ability to find gorgonians and then feed on them. Therefore, abundance could be measured as the number of colonies, their cumulative biomass, or some combination of the two. Since these measures of abundance do not necessarily mirror each other, our estimates of preference could vary depending on the technique used to calculate species abundance. To evaluate the importance of such an effect we analyzed data from one of the sites, Macaroon, using two different indices of gorgonian abundance: the number of colonies, and the sum of the heights of the colonies. The sum of colony heights is an estimator of total biomass. Analysis of the height and total branch length of 1098 5–40-cm tall colonies of three species indicates that height explains 87% of the variation in total colony branch length (Lasker, unpub. data).

The ratio between the number of snails present and that predicted on the basis of host abundance was calculated for each host species using the two indices of host abundance (Table 1). The observed:expected ratios changed markedly when the index of abundance was switched, but there was only a single change in the ranking of host preference. Furthermore, the distributions of snails among the colonies were significantly different from random (G-test) regardless of the abundance index used. As both indices of gorgonian species abundance identified similar preferences, we use numbers of colonies as the index of gorgonian abundance.

The frequency with which the areas were monitored also influences our results. The three-day time interval between samples during the 1984 and 1985 censuses was selected arbitrarily. To determine the degree of bias introduced by this procedure, daily censuses were conducted at Macaroon reef over two four-day periods (April 15–18 and April 20–23, 1985). The total number of moves observed when colonies were censused on a daily basis was 44% greater than that calculated using the censuses from the first and third days. Thus the estimates of movement calculated from the data collected at three day intervals underestimates of the mobility of *C. gibbosum.*

Residence times were compared by analysis of vari-

Table I

Comparison of Cyphoma gibbosum *prey preference at Macaroon Reef during April–June 1985 using two different indices of prey abundance*

| | Relative prey abundance | | Cyphoma observations | | |
| | | | | Preference (observed/predicted) Predicted value based on | |
Species	Number of colonies	Summed colony height	% of occurrences	Number of colonies	Summed heights
Plexaura A	0.347	0.237	1.18	0.03	0.05
Plexaura homomalla	0.057	0.063	13.48	2.37	2.13
Plexaura flexuosa	0.206	0.190	5.78	0.28	0.30
Pseudopterogorgia spp.	0.026	0.036	19.70	7.58	5.47
Pseudoplexaura spp.	0.217	0.378	56.74	2.61	1.50
Other	0.145	0.093	3.11	0.21	0.33

ance. Heterogeneity in variances were eliminated using log transforms. As in the movement data the three day sampling interval may have missed short stays. That error was reduced somewhat by the inclusion of single observations as stays of one day.

The amount of grazing on colonies was also monitored during 1985. Damage to branches was measured as linear centimeters of tissue either injured or removed. On planar surfaces, such as colony bases and *Gorgonia* colonies, areal measurements were made. These measurements were converted to cm^3 of damage using species-specific conversion factors based on a set of more detailed measurements which were also collected in 1985 (see below). Damage on each colony was measured each day snails were present, and a final measurement was taken after all snails had left the colony. Net damage was calculated for each time period as the difference between the successive measurements of damage. *Cyphoma* feeding rates were then calculated by adjusting the net damage for the number of snails present. Since it was impossible to distinguish healed areas or overgrown areas from older scars, they were not included in the final damage measurements. Exclusion of healed and overgrown areas should have led to an underestimate of the damage to the gorgonians. In 19.4% of 543 observations, healing and overgrowth lead to observations in which the total scar length decreased between visits. Feeding rates were set to zero in those cases. (Separate analyses in which those cases were excluded yielded slightly higher average feeding rates, but otherwise paralleled analyses including the cases.)

More detailed estimates of feeding rates were made at Korbiski, Macaroon, Pinnacles, and a fourth reef, Sail Rock, during 1985. Colonies with solitary snails were located and the dimensions of the area of exposed axis were measured to the nearest mm with calipers. The area was again measured the following day and the amount of tissue consumed was determined by subtraction. Thickness of the tissue was also measured to convert the areal measurements into volume measures. Observations were excluded from the analysis if the snail left the colony prior to the second measurement or if a second snail appeared on the same feeding scar.

A second set of detailed observations were again made at Korbiski Reef during May and June 1987. In those observations, detailed measurements of the volume of tissue removed were made on the colonies in the 100 m^2 area at three-day intervals. As in the 1985 measurements, rates were calculated by determining the difference in total damage between the successive measurements and dividing by the elapsed time and the number of snails present. All feeding data were analyzed with analyses of variance using log transforms to reduce heteroscedasticity.

The ash-free dry weight of five of the most common gorgonian species was determined from samples of 10 colonies per species. Single branches were collected, allowed to drip dry (2–4 hours), frozen, and subsequently lyophilized. The axes of the dried specimens were then removed and the sample pulverized with a mortar and pestle. The ash weights of samples were determined by ashing five replicate 5 g samples in a muffle furnace for 4 hours at 450°C. Values were converted to unit volume basis using measurements of branch length and diameter which were made *in situ* at the time of collection.

Results

Distribution and movement patterns

The number of snails identified at the three sites, the average number of snails observed at one time, and the total number of observations are listed in Table II. Abundances of the most common gorgonian species at the three sites are presented in Figure 1. Although the abundances of *C. gibbosum* varied between sites and years the movements of snails were very similar. For in-

Table II

Abundance of Cyphoma gibbosum *at three sites in the San Blas Islands, Panama, during the summer months. See text for exact dates*

	Number/100 m^2 mean (standard error)	Total number marked	Observations per individual	Number of days censused	Inter-colony moves per individual	Total number of observations
Macaroon						
1984	21.5 (1.0)	31	10.2 (0.9)	18	3.3 (0.4)	387
1985	22.3 (0.6)	61	11.2 (0.9)	30	3.6 (0.5)	669
1986	27.9 (1.5)	55	2.7 (0.4)	7	1.6 (0.2)	195
Korbiski						
1984	5.1 (0.1)	10	5.2 (1.6)	18	3.6 (0.2)	91
1985	4.5 (0.3)	14	9.5 (2.2)	26	4.0 (0.8)	117
1986	11.3 (0.8)	20	4.1 (0.4)	7	2.5 (0.3)	79
Pinnacles						
1984	7.3 (0.4)	13	9.4 (1.5)	18	3.9 (0.8)	132
1985	16.5 (0.4)	35	11.5 (1.3)	26	5.0 (0.7)	428
1986	2.7 (0.6)	5	—	7	—	19

stance, a given snail could be expected to appear in approximately 43% of a summer's censuses (41, 39, and 48% at Macaroon, Korbiski and Pinnacles respectively). Similarly the incidence of switching colonies between observations was similar between sites (41%, 54%, and 43%, respectively).

Macaroon

Throughout the study, snails at Macaroon exhibited a strong preference in their occupancy patterns on the different gorgonian species (Fig. 2). Although *Pseudoplexaura* spp. were the most commonly occupied gorgo-
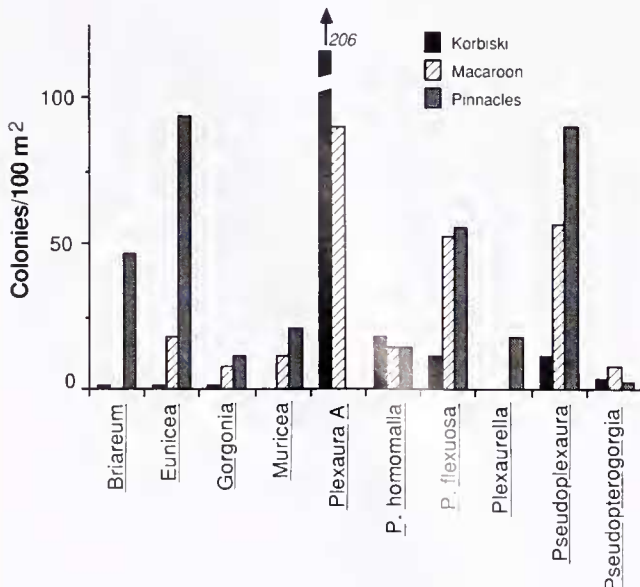

Figure 1. Abundance of gorgonians at three sites in the San Blas Islands, Panama.

nians, when corrected for species abundance the strongest preference was for *Pseudopterogorgia* spp. (Fig. 2). This preference may be attributed to the regular occurrence of a large number of individuals (as many as 12) on a single *P. americana* colony in concert with the low abundance of this species. *Plexaura homomalla* and *Pseudoplexaura* spp. were the next two most frequently preferred species in most years (Fig. 2). In all three years occupancy patterns were significantly different from random (1984, G = 424.8, df = 5, P < 0.005; 1985, G = 601.9, df = 5, P < 0.005; 1986, G = 423.2, df = 5, P < 0.005).

As in the occupancy data, *Pseudopterogorgia* spp. were the most preferred species based on moves to colonies (Fig. 2; 1984, G = 24.67, df = 5, P < 0.001; 1985, G = 67.23, df = 5, P < 0.001; 1986, G = 143.85, df = 4, P ≪ 0.001). *P. homomalla* was preferred in 1984 and 1986 but not in 1985.

In both 1984 and 1985 occupancy preferences were reflected in the amount of time a snail spent on a colony during a single visit (residence time, Table III). The mean number of days a snail remained on a colony was 9.8 (S.E. = 2.9) in 1984 and 6.9 (0.7) in 1985. Residence times were not calculated for 1986 due to the biasing effect of the seven-day interval between observations. The length of stay during any single visit differed between host species in both 1984 and 1985 (ANOVA of log transformed data; 1984, F = 5.10, df = 5,109, P < 0.001; 1985, F = 2.91, df = 5,209, P < 0.025). Visits to *Pseudopterogorgia* colonies, the species preferred on the basis of movements, were longer than those on other species. Visits to *P. homomalla* colonies in 1984 were similar in length to those on *Pseudopterogorgia* and greater than on other species.

Korbiski

The occupancy data indicate that *Pseudopterogorgia* spp. and *Pseudoplexaura porosa* were preferred during
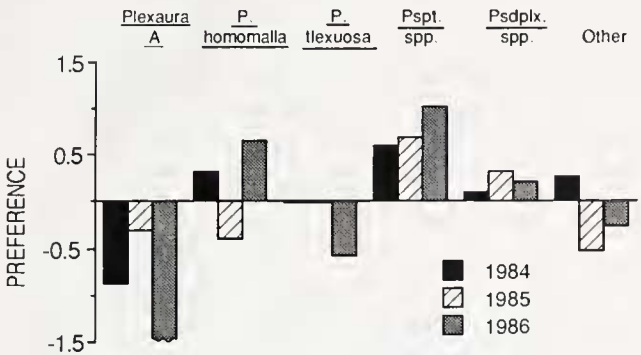
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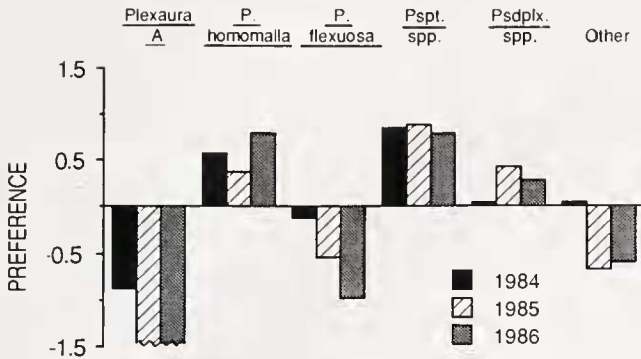
VISITS

Figure 2. Host preferences of *Cyphoma gibbosum* for different species of gorgonian at Macaroon reef. All values are plotted as the log (observed sightings/expected sightings). Cases of no observation are shown as negative preferences extending beyond the scale. Expected observations are predicted from the relative abundance of the gorgonian species. See text for definitions of occupancy and visits.

1984 and 1985 (Fig. 3; 1984, G = 81.6, df = 4, $P < 0.005$; 1985, G = 383.0, df = 3, $P < 0.005$). *P. homomalla* and a single *Briareum asbestinum* colony were preferred in 1986 (Other category in Fig. 3; G = 242.5, df = 2, $P < 0.005$).

As in the occupancy data, *Plexaura* A—the most abundant gorgonian at Korbiski—was visited less frequently than expected. This strong avoidance of *Plexaura* A colonies was the primary factor creating the significantly non-random movement patterns at Korbiski (Fig. 3; 1984, G = 33.24, df = 3, $P < 0.001$; 1985, G = 49.6, df = 3, $P < 0.001$; 1986, G = 154.38, df = 2, $P \ll 0.001$). Positive preferences in movement patterns were variable between years. The most preferred species in the 1984, 1985, and 1986 seasons were *Eunicea* spp., *Pseudoplexaura* spp., and *P. homomalla,* respectively. The preference for *Eunicea* spp. in 1984 was generated by three short visits to *Eunicea* colonies and is not reflected in the occupancy data. Movement preferences in

1985 and 1986 varied between years but were consistent with the occupancy data.

Differences in residence times on colonies were the dominant factors creating differences in the occupancy patterns at Korbiski. In both 1984 and 1985, the gorgonian colonies on which individual snails remained longest were also identified as preferred species by the occupancy data (Fig. 3). Residence time on *Pseudopterogorgia* and *Pseudoplexaura* spp. were longer than on other species in 1984 (Table III, F = 6.45, df = 5,24, $P < 0.05$). These same two species also had the greatest average residence times in 1985, but differences between species were not significant in the more variable 1985 data (F = 0.98, df = 5,45, $P > 0.25$).

Pinnacles

In both 1984 and 1985, the greatest number of *C. gibbosum* sightings were on *Pseudoplexaura* spp. colonies. However, these sightings were only slightly more common than expected on the basis of *Pseudoplexaura* spp. abundance (Fig. 4; 1984, G = 113.1, df = 3, $P < 0.005$; 1985, G = 179.9, df = 5, $P < 0.005$). Snails were preferentially found on *P. homomalla.* Preferences based on movements to different colonies were virtually identical to those found in the occupancy data. Detailed analyses of the 1986 data were not undertaken because there were only 19 sightings of *C. gibbosum* at Pinnacles in 1986.

Table III

Number of days snails remained on colonies during individual visits

| | Length of stay (standard error) | | |
| | Site | | |
	Macaroon	Korbiski	Pinnacles
1984			
Briareum asbestinum	NA	NA	5.6 (0.9)
Eunicea spp.	NA	NA	4.9 (1.3)
Plexaura A	7.4 (3.2)	1.3 (1.1)	NA
Plexaura homomalla	17.1 (4.8)	0.8 (0.1)	9.1 (3.7)
Plexaura flexuosa	6.1 (1.9)	1.1 (0.2)	18.0 (12.0)
Pseudopterogorgia spp.	23.4 (6.0)	2.7 (0.3)	3.0 (0.0)
Pseudoplexaura spp.	9.6 (2.1)	2.8 (0.3)	NA
Other	5.8 (1.9)	0.7 (0.0)	1.0 (0.0)
1985			
Briareum asbestinum	NA		2.7 (1.0)
Eunicea spp.	NA		5.1 (1.1)
Plexaura A	7.8 (5.5)		NA
Plexaura homomalla	5.4 (0.8)		7.7 (2.4)
Plexaura flexuosa	3.9 (0.9)	(1)	3.2 (0.6)
Pseudopterogorgia spp.	12.4	(2.1)	NA
Pseudoplexaura spp.	6.9	.3 (2.8)	5.8 (1.2)
Other		2.2 (0.7)	12.2 (3.6)

NA = species not present or observations lumped in Other category.

KORBISKI

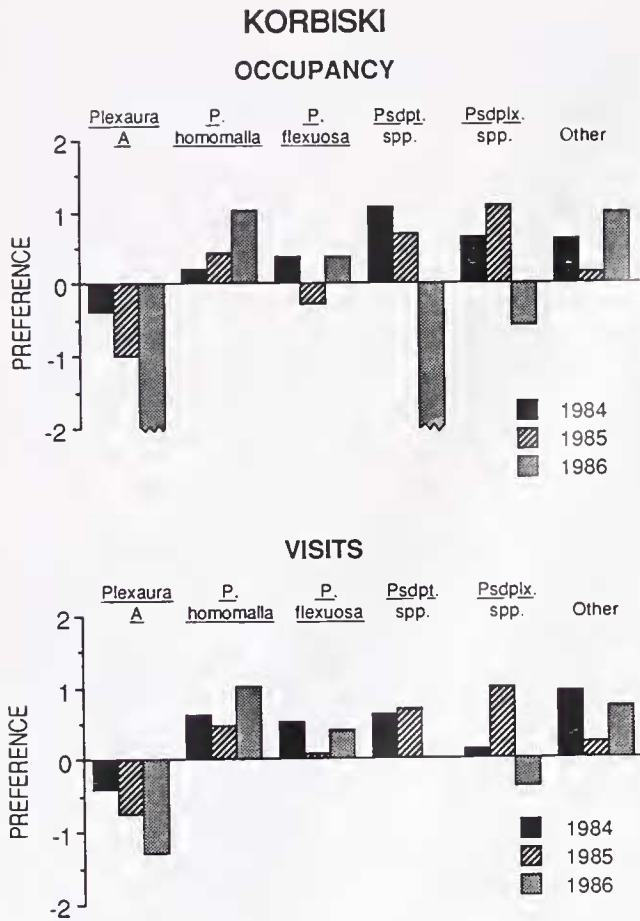### OCCUPANCY

VISITS

Figure 3. *Cyphoma gibbosum* host preferences at Korbiski. See Figure 2 for explanation.

The average stay per visit during 1984 was 9.0 d (S.E. = 3.0) and was 6.2 d (S.E. = 0.8) in 1985. There were no significant differences among species in the number of days a snail remained on a colony (Table III; 1984—F = 0.72, df = 5,48, $P > 0.50$; 1985—F = 1.57, df = 5,142, $P > 0.1$).

Grazing

The feeding rates measured at the three sites during 1985 were extremely variable (Table IV). Feeding rates on some gorgonian species were an order of magnitude greater at Macaroon than at the other sites. Feeding rates between sites and years differed in the relative ranking of the species as well as in the absolute magnitude of the feeding rate. Feeding rates were greatest on *Pseudoplexaura* spp. at Macaroon, *Plexaura* A at Korbiski, and *P. flexuosa* at Pinnacles. The differences in feeding rates were only significant at Pinnacles (F = 3.86, df = 5,218, $P = .002$), and at that site much of the significant result can be attributed to the absence of measurable feeding on *B. asbestinum* colonies. Aside from the comparisons

involving *B. asbestinum* SNK tests indicate that snails at Pinnacles fed at greater rates on *Pseudoplexaura* spp. and on *P. flexuosa* than on "other" species, primarily *Pseudopterogorgia* spp. There were no significant differences between species in feeding rates at Macaroon (F = 2.16, df = 5,265, $P = 0.059$). However, even after transformation feeding rates at Macaroon exhibited significant heteroscedasticity between species (Bartlett-Box F = 4.388, $P < 0.001$).

The most accurate measurements of damage were made in the single day observations of single snails. Four species were compared in those tests, *Pseudoplexaura* spp. (predominantly *P. porosa*), *Plexaura homomalla*, *P. flexuosa*, and *Pseudopterogorgia americana*. Feeding on the different species differed significantly (F = 5.24, df = 3,115, $P = 0.002$). Significantly lower volumes of tissue were grazed from *Pseudopterogorgia americana* colonies than either *P. homomalla* or *Pseudoplexaura* spp. colonies (SNK test, $P < 0.05$). Rates of feeding on *Pseudopterogorgia* spp. and *Pseudoplexaura* spp. colo-
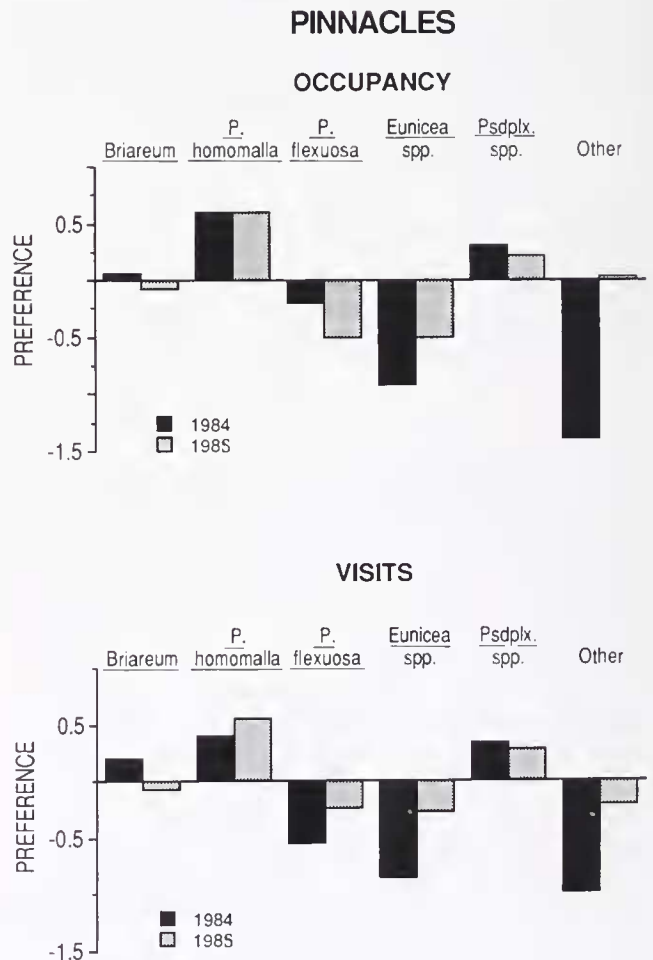
PINNACLES

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VISITS

Figure 4. *Cyphoma gibbosum* host preferences at Pinnacles. See Figure 2 for explanation.

Table IV

Rates of feeding of Cyphoma gibbosum *on different species of gorgonians in the San Blas Islands*

	Damage mm³/Snail/D (standard error)		
	Site		
	Macaroon	Korbiski	Pinnacles
1985			
Briareum asbestinum	NA	NA	8.1 (2.4)
Eunicea spp.	NA	NA	0 (0)
Plexaura A	1.31 (1.31)	10.1 (8.1)	NA
Plexaura homomalla	25.0 (15.9)	2.5 (1.5)	8.4 (2.3)
Plexaura flexuosa	14.6 (5.5)	2.0 (1.1)	14.5 (5.5)
Pseudopterogorgia spp.	40.9 (27.5)	2.0 (1.7)	NA
Pseudoplexaura spp.	343.6 (125.3)	5.3 (1.5)	12.1 (2.1)
Other	54.4 (37.5)	8.1 (8.1)	2.5 (0.9)
1985 Single-day/single-snail observations			
Plexaura homomalla	166.9 (31.4)		
Plexaura flexuosa	199.8 (74.9)		
Pseudoplexaura porosa	277.4 (42.5)		
Pseudopterogorgia americana	81.5 (13.7)		
1987 Korbiski observations			
Plexaura A	168.7 (49.6)		
Plexaura homomalla	137.0 (26.7)		
Plexaura flexuosa	288.2 (46.4)		
Pseudoplexaura porosa	129.7 (47.4)		
Pseudopterogorgia americana	114.7 (56.7)		

NA = species not present or observations lumped in Other category.
Different techniques for assessing damage where employed in 1984 and 1985. See text for method used to estimate feeding rates.

nies were somewhat similar to the measures made at three-day intervals at Macaroon, but most of the single-day/single snail rates were much higher than those made at three-day intervals in 1985.

At first glance, differences between the single-day and three-day interval measurements made during 1985 suggest that healing and overgrowth may have biased the three day interval observations. However, the detailed measurements of feeding scars conducted in 1987 yielded results similar to the single-day observations even though the 1987 measurements were taken at three-day intervals and involved as many as 11 snails on a single colony. This suggests that the lower values of the other 1985 data sets may be attributable to the more rapid but less accurate technique of extrapolating volumes consumed from measurements of feeding scar lengths. Feeding rates on *P. flexuosa* colonies were greater than those on either *Pseudopterogorgia* spp. or on *Pseudoplexaura* spp. (ANOVA, F = 4.33, df = 4,125, $P < 0.003$ and SNK tests $P < 0.05$). In both data sets involving detailed measurements of the volume of tissue consumed, feeding on *Pseudopterogorgia* spp. colonies was lower than that on other colonies.

Table V lists the ash-free dry weight of equal volumes

of tissue of five common gorgonian species. *Pseudopterogorgia americana* and *P. porosa* contained the highest levels of organic matter per unit volume.

Discussion

At the sites in the San Blas, *Pseudoplexaura* spp. (usually *P. porosa*), *Plexaura homomalla,* and *Pseudopterogorgia* spp. (usually *P. americana*) were disproportionately occupied by *C. gibbosum*. Were those patterns indicative of preferences for different species and, if so, were they feeding preferences? We examine these questions in greater detail by breaking the foraging process into its component parts: movement, residence time, and grazing. In each we consider whether sampling errors or social behaviors may have produced patterns which could incorrectly be interpreted as species preferences. We have previously concluded that *C. gibbosum* distribution patterns are affected by such biases (Lasker and Coffroth, 1988). In this article we note such biasing effects and conclude that species preferences also contribute to the distribution patterns. We then consider whether the preferences are also feeding preferences.

Table V

Ash-free dry weight content of five common gorgonians from the San Blas Islands

	Ash-free Dry Weight (mg/mm³)			% Ash-free Dry Weight	
	Mean	Standard deviation	n	Mean	Standard deviation
Plexaura A	0.17	0.04	10	39.6	11.9
Plexaura flexuosa	0.10	0.02	10	15.9	4.2
Plexaura homomalla	0.09	0.06	9	37.7	6.9
Pseudoplexaura porosa	0.20	0.06	10	73.8	6.6
Pseudopterogorgia americana	0.30	0.03	10	73.7	9.0

Movement patterns

The first step in establishing host choice is movement to a colony. Foraging snails can follow one of three general patterns: they may wander randomly until they locate and occupy a colony; they may randomly locate a colony but then occupy it on the basis of some trait of the colony; or they may locate and occupy a colony on the basis of either their own history or the presence or absence of other snails.

The data from San Blas strongly indicate that movement patterns are not random. However, the observed pattern could arise if snails moved randomly but sampled and rejected some colonies on a time scale smaller than the interval between observations. In this case the preferred colonies on which snails remained longer would act as "traps" for the snails. We would find an apparent trend for more moves to some colonies even though the moves had occurred randomly. Sampling at three-day intervals missed as many as 44% of the moves noted in daily monitoring. However, we do not believe the three-day sampling scheme biased the preferences in movements, because the colonies that contained snails in the daily sampling were no different than those identified in the three-day sampling. If our sampling procedure masked random movements, it probably did so by missing cases in which snails left colonies within minutes or hours of their arrival. In observations of snails crawling on the substrate we observed snails to reach a colony, "taste" it, and then move on. Similarly, we observed colonies on which we never found *C. gibbosum* but which exhibited linear patterns of small *C. gibbosum* "tasting" scars (see also Gerhart, 1986). The absence of these sightings in our data set may bias it against finding snails on colonies that were rapidly abandoned. Therefore, the movements reported should be defined as visits, where visits are stays of one or more days. The data clearly demonstrate that *C. gibbosum* visits were not distributed randomly among colonies in the 10 × 10 m sites.

Apparent preferences would also be generated by the presence of snails with home ranges or territories, a phenomena suggested by Ghislein and Wilson (1966). However, our data do not exhibit the patterns of visits that would be expected in a territorial species. If *C. gibbosum* had territories, those snails with territories entirely within the study area should have been observed more often than those snails whose territories only partially overlapped the study area. Thus one would expect to most commonly find rarely appearing snails at the periphery of our areas. To test for this we examined the data for snails that were seen only once, and we compared the proportion of those observations occurring within the central 6 × 6 m of the area (36 m²) to those occurring within the outer 2 m of the area (64 m²). During the 1985 observations at Pinnacles, 13 of 15 single observations occurred within 2 m of the edge (G = 3.91, $P < 0.05$). However, no significant edge effect was observed in the other five data sets (G-tests, all values $P > 0.05$). Some snails appeared to confine their movements to small groups of colonies, but these snails occupied colonies throughout the area, and a snail that was restricted to a small area during one sequence of censuses often appeared at the other end of the 10 × 10 area in the next census. These observations do not exclude the possibility that territories exist, but they indicate that territoriality did not have a great effect on the patterns that we observed.

Apparent species preferences could also occur if snails selected only large colonies and if large colonies were restricted to only a few species. To determine whether the species preferences that we observed were in fact size preferences, we compared the size frequency distribution of the colonies visited to that of all colonies at the site. Since some gorgonian species are consistently smaller than others, analyses combining all species compound size effects with species effects. Therefore, separate analyses for size preferences were conducted for each species for which the colonies covered a range of sizes. When small colonies were present, there were cases of visits and feeding on colonies of all sizes. No significant size preferences were detected among *Pseudoplexaura porosa* and

Eunicea spp. colonies at Pinnacles, nor were size preferences detected among either *P. porosa* or *Plexaura flexuosa* colonies at Macaroon. Larger colonies of *Plexaura* A were preferred at Macaroon. This may reflect the fact that the *Plexaura* A population contained a number of quite small (<30 cm) colonies and these colonies were never the sites of extended visits. Aside from the absence of aggregations on very small colonies there was no relationship between size and the location of *C. gibbosum* aggregations on these species.

Finally *C. gibbosum* may not have been locating specific colonies but rather the presence of other snails. *C. gibbosum* exhibited aggregated distributions at the San Blas Is. sites (Lasker and Coffroth, 1988). Gerhart (1986) reported that *C. gibbosum* recognizes and follows the mucous trails left by other individuals. He proposed that this behavior might explain aggregated *C. gibbosum* distributions. The aggregation of individuals on colonies could exaggerate preferences and possibly generate an appearance of a preference for a species that had initially been chosen at random. Stochastic effects in concert with aggregative behavior undoubtedly contributed to the patterns observed in the San Blas (Lasker and Coffroth, 1988).

Although social interactions affect the distribution patterns in the San Blas, the data also demonstrate the existence of true species preferences. If the observed distributions of *C. gibbosum* were generated by snails following mucous trails and not by species preferences, then at any one time each site should have had several colonies on which groups of snails were present. If there were no species preferences, the location of the aggregations should have changed randomly over time as old trails decayed and "lost" snails located new colonies. Colonies on which more than three snails occurred changed between years. However, the same species were consistently occupied during the different years. During the three summers, 25 different colonies were identified as holding more than three snails. These aggregations lasted for at least two observations and in 1985 one colony contained three or more snails on 18 of the 30 census days. The colonies on which aggregations most commonly occurred were *Pseudoplexaura* (12 colonies), *P. homomalla* (7), and *Pseudopterogorgia* colonies (2). *P. homomalla* and *Pseudopterogorgia* spp. were used in great excess relative to their abundance. *P. porosa* colonies were also used more often than expected, but *P. porosa* usage more closely mirrored local abundance (see also Lasker and Coffroth, 1988).

Residence time

The next component of *C. gibbosum* host preferences is the amount of time a snail remains on the colony, or residence time. Our observations missed extremely short visits. The absence of these very short visits to "non-preferred" species should have biased our data against finding differences in residence times on different colonies. Despite this inherent bias, we observed significant differences in residence time between host species in three out of the six data sets. In those cases where significant differences in residence time were observed, stays on species identified as preferred by the occupancy data were significantly longer than stays on other species. A somewhat similar pattern also was observed among the nonsignificant data sets (Table III).

Gerhart (1986) reports that the length of time *C. gibbosum* individuals remain on *P. homomalla* colonies is reduced if the colony was previously occupied. Our data, which pool observations on many different species, exhibit the opposite trend. The probability of a snail leaving a colony was calculated by considering each observation of a snail on a colony as a replicate case. Cases were partitioned between colonies with only one snail present and those with more than one snail. The probability of leaving a colony was not positively associated with the presence of other snails (G-test, $P > 0.05$ in 8 data sets - Korbiski and Macaroon 1984, 1985, 1986, Pinnacles 1984, 1985). During 1985 the year with the greatest number of observations a significant positive association was found between the presence of other snails and remaining on a colony (G- tests, $P < 0.025$, all three sites). Colonies on which individuals remained for long periods of time were also the colonies that the most snails visited. This pattern was repeated at all of the sites in all years. At each site there was at least one colony that snails frequently visited, and on which they invariably remained for extended periods. In several cases these colonies were sites for egg deposition or were occupied by juveniles (snails <1 cm length). The colonies with the longest history of occupancy by *C. gibbosum* and on which *C. gibbosum* had the longest residence times were invariably *P. porosa* and *P. americana*. The most "popular" of these colonies, a *P. americana* at Macaroon, has contained groups of 2–12 snails for 7 years. Although our results differ from Gerhart's (1986), his study only examined *P. homomalla*, whereas our data include observations from other species. Unfortunately our data contained too few observations of snails on *P. homomalla* to directly test Gerhart's experimental results.

Grazing rates

The final component of the feeding process is the grazing rate. As we have already discussed some of the variance in the 1985 observations made at three-day rates may be measurement error. However, detailed measurements made in the 1985 single-snail/single-day observa-

tions and again in 1987 are also characterized by tremendous variability. Much of this variability can be attributed to the fact that gorgonians are not only feeding sites, and that much of the time spent on a colony is not used for feeding. We frequently observed snails laying eggs, mating, or simply "sitting" in the middle of feeding scars. The effect of social behaviors is suggested by the presence of a significant *negative* correlation between the feeding rate on a colony and the number of snails present (Korbiski, 1987, r = −0.18, n = 130, P = 0.019).

The one trend appearing consistently was the lower feeding rates observed on *Pseudopterogorgia* colonies. If the volume consumed was dependent on the number of "bites" taken or the time spent actively feeding, these data suggest an aversion for *Pseudopterogorgia* as a food source. Thus the data on feeding rates only partially agree with the distribution patterns.

The rate at which *C. gibbosum* feed in conjunction with the amount of time a snail spends on a colony defines the total amount of tissue that a snail ingests. *Plexaura homomalla, Pseudoplexaura porosa,* and *Pseudopterogorgia americana* were the most commonly occupied gorgonians, and therefore *C. gibbosum* fed more often on these species than other species. If the trends in feeding rates are also considered then we can tentatively conclude that *Pseudoplexaura* spp. and *P. homomalla* made up the greatest proportion of the *C. gibbosum* diet.

What drives Cyphoma gibbosum *host preferences?*

The movement and residence preferences create a pattern of feeding in which the species preferred on the basis of occupancy make up the greatest proportion of the *C. gibbosum* diet. Therefore we will first consider the hypothesis that the movement and feeding patterns of *C. gibbosum* are dietary preferences based on prey quality.

Quality of gorgonians as prey species can be divided into two categories: nutritive content and defensive quality. Nutritive content in turn can be divided into the absolute food content of the gorgonian and the different types of compounds present. When expressed as a percentage of the ash free dry weight of the tissue there are not large differences in the protein, lipid, and carbohydrate content of the different gorgonian species (Lasker, unpub. data). However, there are large differences in the sclerite content of the different species. Thus, the greatest difference in the nutritive value of the different species is in the organic content of the tissue. *Pseudopterogorgia americana* and *P. porosa,* the species with the highest levels of organic matter per unit volume (Table V), were preferentially occupied by *C. gibbosum.* Even after adjusting for the lower feeding rates on *P. americana, C. gibbosum* would have a higher rate of organic intake on these species than on the other gorgonian species. Furthermore, feeding on these two species would allow snails to obtain a given amount of nutrition in the smallest amount of time. Thus *Pseudopterogorgia americana* and *Pseudoplexaura* spp. should be preferred if *C. gibbosum* foraged in a manner that either maximized organic intake or minimized foraging time. However, *P. homomalla*—the other frequently occupied species—had the lowest average organic content, and would be a poor food choice under either of the foraging criteria. Organic content may play a role in establishing preferences, but it does not explain all of the observed pattern.

The low levels of feeding on *Plexaura* A and *P. flexuosa* also suggests that sclerites could act as a deterrent to feeding by *C. gibbosum.* Harvell and Suchanek (1987) suggest the presence of such a relationship in the feeding rates that they measured. However, in the San Blas, *P. homomalla* was eaten regularly despite its high sclerite content (sclerites make up the major portion of the ash component of gorgonian tissue). Furthermore, feeding rates on *P. flexuosa*—the species with the highest ash content—were high in 1987. Again, there is some correspondence between feeding and sclerite content, but our data indicate that sclerite content alone is a poor predictor of *C. gibbosum* foraging behavior.

The presence of chemical defenses within the gorgonians also fails to explain the observed feeding preferences. Many authors have commented on the presence of secondary compounds in gorgonians (Ciereszko and Karns, 1973; Tursch *et al.,* 1978; Lee *et al.,* 1981; Fenical, 1982; Gerhart, 1984), and both *P. homomalla* and *P. porosa* contain toxic compounds. *P. homomalla* contains impressive quantities of the prostaglandin PGA_2 (Schneider *et al.,* 1977; Gerhart, 1984, 1986), and *P. porosa* contains crassin acetate (Lee *et al.,* 1981). Both of these compounds have toxic effects on organisms (PGA_2—Gerhart, 1986; crassin acetate—Perkins and Ciereszko, 1973; Lee *et al.,* 1981). Although we do not know what compounds may be in the other gorgonian species, it is clear that *C. gibbosum* is neither picking its prey nor adjusting its feeding rate to avoid the toxin in these two species. If chemical defenses affect *C. gibbosum* feeding, then additional factors such as the snail's resistance to given defenses must also be considered.

There is some correspondence between the occupancy patterns and the nutritive quality of their gorgonian prey. However, the observed preference for *P. homomalla* colonies as well as the inconsistencies in observed feeding rates suggest that additional factors affect *C. gibbosum* movement and residence patterns. As alternatives to feeding preferences we consider the hypotheses that *C. gibbosum* choose gorgonians on the basis of their suitability as sites for egg laying and/or as sites for predator avoidance.

C. gibbosum deposit their eggs on the bare axis of gor-

gonians, which are exposed by the snails' feeding activities. At some of the sites the colonies chosen for egg laying paralleled the occupancy preferences, but the trends in egg laying were poor predictors of occupancy preferences. Egg laying was observed on *Plexaura homomalla, Pseudoplexaura porosa, Pseudopterogorgia americana, Plexaura flexuosa,* and a *Eunicea* sp. At Macaroon eggs were most frequently deposited on *P. porosa* colonies (13 of 16 observations of newly laid eggs)—a species also preferred based on the occupancy data. However, at Pinnacles, a site in which *Pseudoplexaura* spp. were preferentially occupied, those species were never used for egg deposition. Similarly, *Pseudopterogorgia americana* was frequently occupied at Macaroon but was only used for egg deposition on one occasion. *Eunicea* spp. were most commonly used for egg deposition at both Pinnacles and Korbiski, but overall host use mirrored egg laying on *Eunicea* spp. in only one instance, Korbiski, 1986. The small number of snails engaged in egg laying at the three sites (no more than 4 each at Pinnacles and Korbiski and 16 at Macaroon) makes it difficult to determine with confidence whether distinct egg laying preferences exist. However, the data indicate that the distribution patterns observed were not driven by preferences for sites of egg deposition.

Another hypothesis that could explain movement patterns is based on the protection different host species offer. Predation is an important source of mortality in the San Blas. Mortality averaged 18.3%/year at Macaroon and 6.8%/year at Pinnacles (Lasker and Coffroth, 1988). Shell debris from mortality events suggests that crabs, stomatopods, and fishes are responsible for 60% of the mortality.

The largest and most stable aggregations of *C. gibbosum* occurred on *P. americana* colonies. This species was only used for egg deposition once and was grazed at a lower rate than other gorgonians. *P. americana* colonies are large and structurally complex, and *C. gibbosum* located in *Pseudopterogorgia* colonies are difficult to find. This may protect snails from visual predators such as fishes. Higher survival might also account for our frequent observations of small snails on these colonies.

Predator avoidance might also be the basis for the occupancy of *P. homomalla* and *Pseudoplexaura* spp. colonies. Gerhart (1986) showed that fish find the mantle of *C. gibbosum* distasteful, and suggested that *C. gibbosum* coloration and aggregations warn potential predators of the presence of toxic compounds which the snail has obtained from its food sources. Schneider (1972, in Steudler *et al.,* 1977) isolated the prostaglandin PGB_2 from *C. gibbosum* tissue and suggested that the gorgonian prostaglandin PGA_2 was a likely precursor of this secondary compound. The *C. gibbosum* host preferences observed in the present study are clearly compatible with Gerhart's hypothesis.

The distribution of *C. gibbosum* on its gorgonian prey exhibits a complex pattern reflecting the snail's use of the gorgonian as both prey and host. We found no correlation between known chemical defenses and *C. gibbosum* feeding, but the preferential use of some gorgonian species correlated with their organic content/structural defenses. This suggests that food quality plays a role in determining *C. gibbosum* distribution patterns. However, the poor correspondence between distribution patterns and feeding rates suggests that additional factors play as great a role as feeding in establishing *C. gibbosum* foraging behavior. Additional factors that may explain some aspects of the snail's distributions should be explored in future research. These are: the possible protective role of the host colony, the social interactions which generate the aggregative behavior, and intraspecific variation between gorgonian colonies which could explain why only a small subset of gorgonian colonies serve as aggregation sites.

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